# THE STATUS OF NITROGEN IN THE HAWKESBURY SANDSTONE SOILS AND THEIR PLANT COMMUNITIES IN THE SYDNEY DISTRICT. II.

## The Distribution and Circulation of Nitrogen.

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(Two Text-figures.)

[Read 30th April, 1958.]*

*Synopsis.*

The nitrogen content of a typical Hawkesbury Sandstone ecosystem is estimated to be approximately 2,400 lb. per acre. It is fractionated in the rooting medium, living plant tissue and plant litter in the ratio of 200 : 35 : 1. On the basis of estimates of nitrogen release from the soil organic matter complex and measurements of litter returns (700 lb. per acre per annum), it appears that an annual cycle of 2-3 lb. nitrogen per acre occurs. These values for *Eucalyptus* forest on Hawkesbury Sandstone are shown to be low in comparison with other types of forest. The litter accumulated on the forest floor occupies only 0·5% of the nitrogen capital of the sandstone ecosystem and proportionately greater amounts of nitrogen are contained in living plant tissue than are found in pine forests.

### Introduction.

An earlier paper (Hannon, 1956) described the concentration values of nitrogen in the parent rock, the soil and the plant material of the naturally occurring communities on Hawkesbury Sandstone in the Sydney district. In the present instance, an attempt will be made to convert these concentration values into absolute terms to allow the estimation and fractionation of the nitrogen capital of the ecosystem. This conversion is necessary to provide a concrete expression of the nitrogen content of the communities and to allow comparison with other ecosystems.

Estimates of this nature are relatively simple in pot trials where the initial quantities of the various component fractions may be calculated, the growth rate accurately measured, the losses accounted for and final computations compared with the initial. Even in field trials, a certain acreage is sown uniformly with a single variety at a given time. The sandstone communities, however, are very complex. Although heaths and scrubs of long-lived shrubs and relatively uniform structure do occur, the most widely spread formation is the *Eucalyptus* forest. Like the scrubs, the forests are characterized by a great variety in their species composition, but possess both shrub and tree layers. These communities are composed of individuals of different physiological age and of diverse genetic constitution. Stands of the same formation frequently display appreciable variation, especially in relation to aspect effects or the stage of regeneration from fire. Difficulties, which will be mentioned later, also apply to the study of the rooting medium and the litter fraction. All of these factors complicate a study of nutrient distribution, which, to be complete, requires detailed and quantitative analyses of typical stands. In the absence of these observations, only approximations and estimates can be made. These will, however, provide useful information.

### The Distribution of Nitrogen.

The physiography of the sandstone-covered areas allows a division into three major ecological niches—the undissected portions of the plateau surface, the gully slopes, and the gully floor. The plateau surface typically bears heath, scrub, tree-scrub or low scrub forest. These are the least luxuriant of the sandstone formations and are the communities in which exposure effects play a significant role. At the other extreme, the tallest forests, containing a more mesomorphic understorey, are found only on the

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gully floor. Here not only are exposure effects eliminated, but plant nutrient and water supply are increased by accumulation from the surrounding ridges and slopes. In both of these niches the soil cover is better developed than on the slopes—on the plateau, because erosive forces have not been so active, and on the gully floor because accumulation has occurred from topographically higher areas.

It is thus obvious that, on the plateau, exposure effects complicate the existence of a direct relationship between plant development and soil nutrient levels. When the distribution of nutrients is under consideration, it is logical to select an example where soil nutrient supply rather than any other factor of the environment is limiting plant development. On the other hand, the gully floors occupy a very small percentage of the total area where sandstone outcrops and cannot therefore be taken as typical of the sandstone areas as a whole.

The gully slopes are usually occupied by tall scrub forest. This is a very widely spread formation occurring chiefly on slopes where conditions of shelter and soil moisture are favourable. It is restricted to the lower portions of the sunny-north-facing slopes, but may extend to the top of the gully on south-facing slopes. It also occupies the restricted areas on the upland plateau where exposure is not too rigorous.

The plateau, composed chiefly of Hawkesbury Sandstone, which encircles the Sydney Plains, is very dissected, particularly to the west and north of Sydney. To the south, on the Nepean Ramp, dissection is not so marked as in the other areas, but occurs extensively. The physiography thus presents areas of very considerable size which are topographically suited to tall scrub forest development.

An illustration of the distribution of nitrogen amongst the three major divisions of the ecosystem—the rooting medium, the undecomposed plant litter and the plants—will therefore be given by considering a hypothetical stand of the poorer quality of tall scrub forest formation. This stand would be described as "average" with respect to its plant and litter cover, its soil depth and the nitrogen concentrations of its mineral and organic components. No information is available to permit the inclusion of the animal life of these communities.

### *Methods of Estimation.*

Part of the data used in making this calculation has been previously presented (Hannon, 1956—Tables 3–8, 14–18). Part is given in Tables i–iii of the Appendix (pp. 83–84, below) and details concerning the estimation of soil and plant mass will now be discussed.

A visual method of weight estimation of plant cover was employed, and attention was confined mainly to the shoot systems. After estimation, shrub species were frequently cut at ground level and the estimates checked on a spring-balance. Experience in the estimation of tree mass was gained in areas of private property where the trees were being felled and weighed to be sold for pulp and firewood. Corrections were applied to convert these values to an oven-dry basis.

The figure for litter mass was obtained by direct measurement of the total litter collected from a number of areas. A correction was applied to these values to allow for the fact that outcropping rock surfaces, tree bases and shrub cover prevent the accumulation of litter over the entire surface in these communities.

Soil depth, the occurrence of rock floaters and the rooting habits of the plant cover have been examined in excavation works made by the Metropolitan Water, Sewerage and Drainage Board in areas of Hawkesbury Sandstone. Even on the plateau surface, soil depth generally does not exceed 24″–30″ and rock floaters commonly occur, mixed with the soil, above the underlying layer of almost solid rock. The soils on the gully slopes are very skeletal. Rock boulders outcrop over most of the surface and, apart from very isolated pockets which may extend to 5–6 feet, soil depth is very shallow. Usually pockets barely exceed 12″. Inspection at the ground surface level and by using an iron bar to test soil depth indicates that soil occupies only a very small percentage of the rooting medium. However, when large areas have been excavated with the assistance of heavy drilling and blasting equipment, it is obvious that greater amounts of soil are to be found underlying the floaters than casual inspection would have suggested. Close examination of this material, however, shows that small rock fragments and pulverized rock which have originated in the drilling and blasting operations are contributing to this fraction. The soil cover is variable from one patch to another, but usually occupies no more than 40% of the rooting medium volume.

The rooting habits of the trees occupying these areas are remarkable. Main tap roots are not found and usually a division into three or four major roots occurs at the stem base. These spread laterally along the rock surface to a point where jointing occurs. The roots penetrate downwards through fissures—instances have been observed where the root is flattened to only half an inch in thickness and is of a width of 12 inches to allow its passage through the rock layers. The interweaving of the roots through the rock crevices must provide a very firm anchorage. It is obvious that penetration by tree roots frequently is a factor of importance in the fracture of the sandstone. The great bulk of the feeding root zone is found in the surface layers but a few large roots may extend to depths of up to ten feet or more to allow for support and the absorption of water. For the present purpose, a soil depth of 20 inches will be chosen, since only occasional roots are found beyond this depth and their absorptive surfaces are restricted to their extremities; in addition, soil nitrogen levels are very low below this depth. The region occupied by the feeding roots is of the greatest relevance to the present consideration of the soil–plant–litter system.

On the basis of these measurements and observations, the nitrogen capital of a typical stand of tall scrub forest on Hawkesbury Sandstone has been estimated as follows:

*Calculation of the Nitrogen Content of a Hawkesbury Sandstone Ecosystem.*

1. *The Rooting Medium* (60% rock+40% soil).

| Depth of Sample. (in.) | Volume per Acre Surface. (cu. ft.) | Density. (lb./cu. ft.) | Mass. (lb.) | Nitrogen Concentration. (p.p.m.) | Nitrogen Content. (lb.) |
|---|---|---|---|---|---|
| Rock: | | | | | |
| 0–20 .. .. | 43,560 | 130·8 | 5,697,648 | 180 | 1025·6 |
| Soil: | | | | | |
| 0–8 .. .. | 11,616 | 87·2 | 1,012,915 | 500 | 506·5 |
| 8–20 .. .. | 17,424 | 93·5 | 1,629,144 | 300 | 488·7 |
| Rock+soil .. .. | — | — | — | — | 2021 |

2. *The Litter Fraction.*

| Fraction. | Mass per Acre Surface. (lb.) | Nitrogen Concentration. (p.p.m.) | Nitrogen Content. (lb.) |
|---|---|---|---|
| Total litter .. .. | 5,600 | 2,000 | 11 |

3. *The Plant Cover.*

Mass per acre of plant material: 70 tons.
Composition: 5% living shoot and root tissue.
95% woody tissue.

| Fraction. | Mass per Acre Surface. (lb.) | Nitrogen Concentration. (p.p.m.) | Nitrogen Content. (lb.) |
|---|---|---|---|
| Living tissue .. | 7,840 | 7,000 | 54·9 |
| Woody tissue .. .. | 148,960 | 2,000 | 297·9 |
| Total .. .. | 156,800 | — | 353 |

Total nitrogen content of ecosystem=2,385 lb./acre.

The calculation shows that in this stand the nitrogen capital approximates 2,400 lb. per acre and that the proportion of the nitrogen contained in the rock + soil, plants and litter is in the ratio of approximately 200:35:1. Even though the presence of the mineral fraction reduces the concentration of nitrogen in the rock and soil to a level far lower than that of the organic material of the plant and litter, the very great mass of rock and soil in comparison to the other fractions renders it the chief reserve of nitrogen (and other nutrients) in these communities.

## The Circulation of Nitrogen.

The foregoing fractionation illustrates the static distribution of nitrogen in the ecosystem. The dynamic aspect — that of the interchange of nitrogen between the three major fractions of the rooting medium, plants and litter — requires consideration also. This cycle may be complicated by internal cycles within each of the three fractions, e.g. the withdrawal of nutrients into a plant from senescent leaves, but the fundamental principles of nutrient circulation may be summarized in broad outline by the following items:

1. The release of nitrogen from the soil organic matter complex resulting in the formation of an "available" form of nitrogen.
2. The absorption, translocation and synthesis of available nitrogen by plants, resulting in plant growth.
3. The maturity and senescence of plant organs, resulting in litter formation.
4. The partial decomposition of litter, resulting in its incorporation into the soil organic matter complex.

Little detailed information is available on these aspects of nutrient circulation in Hawkesbury Sandstone communities, but certain data have been collected and will permit discussion in generalized terms.

### *The Release of Nitrogen from the Soil Organic Matter Complex.*

Discussion of Data.

On the basis of data presented previously (Hannon, 1956—Table 13), it may be calculated that over a period of one year available nitrogen is released from the sandstone soil organic matter reserve in a concentration of approximately 100 parts per million of soil. This value was obtained by bio-assay under conditions where temperature, water and the nitrogen-free mineral supply were close to optimal. After correction for growth due to the seed reserves, plant growth showed an approximate three-fold increase in the presence of a nitrogen-free mineral solution over that where only water had been added. This may be used as an approximate indication of the extent to which the mineral supply stimulated the nitrification rate. Even this latter value should be reduced since, under field conditions, water supply is very spasmodic and must limit the activity of the microorganisms engaged in organic matter conversions. Under field conditions an annual release of nitrogen in available form in a concentration of approximately 25 p.p.m. of soil might thus be anticipated.

Field observations show that a plant whose shoot system occupies one square metre of surface may be assumed to bear a root system, the extremities of which penetrate a volume of 3 × 3 × 0·25 cubic metres of soil and rock. With an apparent density of 1·4 g. per c.c., the 40% of this volume occupied by soil would weigh 1,260,000 g. On the basis of the above-mentioned assumptions, from 1,260,000 g., 31·5 g. available nitrogen would be released each year.

However, the proportion of soil within the absorptive range of the roots will be of greater relevance than the volume through which the roots extend. In addition, the form in which the nitrogen becomes available, particularly whether it is freely mobile as is nitrate or adsorbed as is ammonia, must be considered. The sparsity of nitrate in the soils other than in swamps, and the consistent presence of ammonia would indicate that the latter is the more likely form. Furthermore, the possibility cannot be overlooked that forms of nitrogen and of other nutrients not considered "available" for the growth of mesomorphic species may be acceptable to sclerophyllous vegetation under natural conditions when more easily assimilable sources are not available. Since absorption of nutrients occurs only in regions close to the actively growing root tips which, in woody perennial species, form a small percentage of the total root mass, it is very probable that absorption may occur from only 1% of the total volume penetrated by the roots. The volume through which the roots pass is shared with the root systems of adjoining shrubs. Certain quantities of available nitrogen would also be required by soil-inhabiting microorganisms and some may be lost from the ecosystem by various factors which will be discussed later.

In view of these considerations, 0·315 g. available nitrogen may be absorbed by the shrub during one year. Knowledge of the concentration of nitrogen in plant tissue enables the calculation of the mass of tissue produced by the incorporation of this quantity of nitrogen into new growth. On the basis of an average value of 4,000 p.p.m. nitrogen for the tissues of the root, stem and leaf, a mass of approximately 79 g. per square metre of tissue could be developed from 0·315 g. of available nitrogen. On the basis of this figure, an amount of 700 lb. per acre (0·31 ton per acre) is suggested as the annual production of organic matter. An unknown fraction of this quantity would be diverted to the extension of the root system. Jenny (1941) quotes the work of German investigators who have recorded that in forests the weight of the underground mass of vegetation is from 20% to 30% of the total mass; 10% is often quoted in the literature. On the basis of the very few studies where roots were sampled, Rennie (1955) notes that of the total nutrients taken up by trees, 13% was the average quantity present in the roots.

TABLE 1.
(Taken from Jenny, 1941.*)
*Organic Matter Production by Vegetation.*
(Roots not included unless stated.)

| Type of Vegetation. | Annual Production. (Tons/acre.) | Remarks. |
|---|---|---|
| Alpine meadows .. .. | <0·22–0·40 | Clipped quadrats, Poland, air-dry (includes moss, lichens). |
| Short-grass prairie .. .. | 0·71 | Clipped quadrats, Colorado, air-dry. |
| Mixed tall-grass prairie .. | 2·22 | Clipped quadrats, Nebraska, air-dry. |
| Tall-grass prairies .. .. | 0·85–1·73 | Annual prairie hay figures, Middle West. |
| Average forest (leaves, wood, twigs) .. .. .. .. | 2·67 | German forests, air-dry. |
| Beech: | | |
| Wood .. .. .. | 1·42 | Central Europe, air-dry. |
| Leaves .. .. .. | 1·47 | |
| Pine: | | |
| Wood .. .. .. | 1·42 | Central Europe, air-dry. |
| Needles .. .. .. | 1·42 | |
| White-pine needles .. .. | 2·09 | Connecticut, 1934, oven-dry. |
| Beech—birch—aspen forest .. | 2·85 | Leaf litter only, Germany, air-dry. |
| Tropical primeval forest (leaves, trunks, roots) .. .. .. | 11·1 | Java, estimate, moist. |
| Tropical legumes .. .. | 24·4 | Dutch East Indies, moist. |
| Tropical savannas .. .. | 13·3 | Estimate, moist? |
| Monsoon forest .. .. .. | 22·2 | Estimate, moist? |
| Tropical rain forest .. .. | 45–90 | Estimate, moist? |
| *Eucalyptus* scrub forest .. | 0·31 | Estimate, oven-dry, roots included. |

* An estimate for a Hawkesbury Sandstone community is included for comparison.

Plant cover is not uniform or even continuous in the sandstone communities. It is very probable, however, that the areal extent of bare ground is counterbalanced by the interlacing of the shoot systems. This and the other limitations of this calculation are realized; many assumptions have had to be made. Nevertheless, each of the assumptions has been carefully considered in light of the known facts and observations. Pending fuller investigation of nutrient — and in particular, nitrogen — circulation in these communities, the calculation is of value in setting an approximate level of the quantities involved, and emphasizing the gaps in our present state of knowledge. It is of interest to compare this estimate with the figures compiled by Jenny (1941) of the annual organic matter production by varying types of vegetative cover. These values are shown in Table 1. It is seen that organic matter production in Hawkesbury Sandstone communities is only small by comparison on these standards.

### *Plant Growth Rate.*

Observations of the growth rate of sandstone species are restricted to a few measurements of shoot expansion in the shrub stratum over a period of one year. Variation in the expansion of different shoots on the same individual and between different individuals of the same species and similar age was very marked. Consequently these values do not form a satisfactory basis for a measurement or an estimate of the annual production of plant tissue, especially since no attention has been paid to the dominants of the widespread forest communities—*Eucalyptus* and *Angophora* trees.

TABLE 2.

*Litter Fall in Forest Communities on Hawkesbury Sandstone.*

Collections made in low scrub forest, Warrah Sanctuary.

| Period and Season of Sampling. (Month.) | Dry Weight of Litter at Each Site. (g./sq. yd.) | Total Weight of Litter at Each Collection. (g.) | Total Area of Sample. (sq. yd.) | Total Leaf Litter. (g.) | Total *Eucalyptus* Leaf Litter. (g.) | Total *Angophora* Leaf Litter. (g.) |
|---|---|---|---|---|---|---|
| 4 (July–November) | (*a*) 19·58<br>(*b*) 24·02<br>(*c*) 1·62<br>(*d*) 13·26 | 58·5 | 4 | 33·0 | 13·7 | 19·3 |
| 2 (November–January) | (*a*) 10·48<br>(*b*) 7·37<br>(*c*) 1·57<br>(*d*) 4·07 | 23·5 | 4 | 21·2 | 11·9 | 9·3 |
| 3 (January-April) | (*a*) 13·46<br>(*b*) 9·02<br>(*c*) 6·45<br>(*d*) 4·21 | 33·1 | 4 | 20·5 | 10·9 | 9·6 |
| 4 (April–August) | (*a*) 6·90<br>(*b*) 6·33<br>(*c*) 1·80<br>(*d*) 8·97 | 24·0 | 4 | 10·8 | 4·6 | 6·2 |
| 1 (August–September) | (*a*) 8·15<br>(*b*) 3·73<br>(*c*) 14·48<br>(*d*) 0·91<br>(*e*) 4·15<br>(*f*) 5·73 | 37·2 | 6 | 30·9 | 6·1 | 24·8 |
| 1 (September–October) | (*e*) 15·05<br>(*f*) 20·49 | 35·5 | 2 | 26·8 | 10·8 | 16·0 |

### *Litter Fall.*

In a community which is in equilibrium with its environment, the amount of growth produced per annum must be approximately equivalent to the annual litter fall. On theoretical grounds a net gain or net loss does not occur in a mature community. Consideration of this fact somewhat reduces the shortcomings of the foregoing data on organic matter production in these communities, both in the theoretical calculation and in the measurements of the expansion of the shoot systems under field conditions.

### Presentation of Data.

Litter collections have therefore been made in sandstone communities and the results are presented in Tables 2, 3 and 4.

Each site was chosen as being typical of the structure and floristics of the stand, but variation in the litter collections from plot to plot is very marked; this may reflect the influence of the direction of the prevailing winds. However, the data clearly demonstrate that the amount of litter falling in these *Eucalyptus* forests is uniformly low. Similar results were obtained with all the types of collecting agencies used — wooden trays with a fine wire base, supported two inches above ground level, hessian pegged flat onto the ground surface, and the ground surface cleared of litter.

The large-leaved tree species — *Eucalyptus* and *Angophora* — provide practically all of the litter in the form of leaves and twigs. The contribution from shrubs in areas other than directly beneath them is negligible. Apart from certain of the larger shrubs, only seldom is any accumulation of leaf litter found at their base. The microphyllous leaves of most shrub species would be difficult to detect when scattered amongst the general litter accumulated on the ground surface, and were not found

TABLE 3.

*Litter Fall in Forest Communities on Hawkesbury Sandstone.*

Collections made in tall scrub forest, Kuring-gai Chase.

| Period and Season of Sampling. (Month.) | Dry Weight of Litter at Each Site. (g./sq. yd.) | Total Weight of Litter at Each Collection. (g.) | Total Area of Sample. (sq. yd.) | Total Leaf Litter. (g.) | Total *Eucalyptus* Leaf Litter. (g.) | Total *Angophora* Leaf Litter. (g.) |
|---|---|---|---|---|---|---|
| 2 (March–May) | (*a*) 7·6<br>(*b*) 1·77<br>(*c*) 1·14<br>(*d*) 1·01 | 11·5 | 4 | 3·6 | 1·3 | 2·3 |
| 2 (May–July) | (*a*) 5·87<br>(*b*) 3·16<br>(*c*) 3·64<br>(*d*) 8·66 | 21·3 | 4 | 2·9 | 1·4 | 1·5 |
| 4 (July–November) | (*a*) 31·91<br>(*b*) 23·87<br>(*c*) 15·25<br>(*d*) 19·65 | 90·7 | 4 | 36·0 | 3·2 | 32·8 |
| 4 (November–March) | (*a*) 4·37<br>(*b*) 6·84<br>(*c*) 7·19<br>(*d*) 5·78 | 24·2 | 4 | 6·1 | 1·2 | 4·9 |

in any abundance on hessian placed around the stem base and underlying the canopy of individual shrubs. The litter collected here consisted mainly of defoliated fine twigs. The quantities of litter collected beneath shrubs are given in Table 4 and are seen to be quite appreciable. The values shown in Table 4 are not representative of the whole shrub stratum, since bulky species, as *Banksia serrata* and *Banksia ericifolia*, while common, are not typical of much of the shrub stratum. *Epacris pulchella* on the other hand is less vigorous than the average shrub cover. On the basis of the figures shown in Table 4 and acquaintance with the sandstone communities, an average value of approximately 10–15 g. per sq. yd. (140 lb. per acre) for the total yearly fall would be suggested from the shrub layer. This estimate appears low in light of the values shown in Table 4, where the figures refer to monthly collections, but inspection of the growth form of many shrub species and observations of their growth habit indicate that major growth bursts and litter fall occur but once each year. Evidence to be presented later shows that leaf fall from trees is at its peak at the season when the shrub litter was collected. A further factor which will reduce the values in Table 4 is that the shrub stratum is not continuous.

A considerable proportion of bare space occurs between shrubs, particularly in the forest formations and, in addition, part of the area is occupied by outcropping rock and the trunks of the trees.

TABLE 4.
*Litter Fall from Shrub Stratum.*
Finely woven hessian was pegged onto the ground surface beneath the shrub canopy in a low scrub forest stand in Warrah Sanctuary.

| Composition of Shrub Stratum. | Period and Season of Sampling. (month.) | Total Dry Weight of Litter. (g./sq. yd.) | Remarks. |
|---|---|---|---|
| *Banksia serrata* 10 ft. tall ; *Boronia ledifolia* ; *Dillwynia ericifolia* ; *Isopogon anemonifolius* | 1 (July–Aug.) | 13·72 | |
| | 1 (Aug.–Sept.) | 57·64 | Mostly bark and twigs from *B. serrata.* |
| | 1 (Sept.–Oct.) | 30·60 | Mostly bark and twigs from *B. serrata.* |
| | 1 (Oct.–Nov.) | 8·39 | |
| *Banksia ericifolia* ; *Hakea teretifolia,* 3 ft. 6 in. high. | 1 (July–Aug.) | 5·65 | |
| | 1 (Aug.–Sept.) | 27·86 | Almost entirely twigs from *B. ericifolia.* |
| | 1 (Sept.–Oct.) | 10·06 | |
| | 1 (Oct.–Nov.) | 2·84 | |
| *Epacris pulchella* cluster of bushes averaging 30 in. | 1 (July–Aug.) | 0·07 | |
| | 1 (Aug.–Sept.) | 1·14 | Fine twigs bearing few leaves. |
| | 1 (Sept.–Oct.) | 3·64 | |
| | 1 (Oct.–Nov.) | 1·00 | |

Inspection of Table 5 suggests that leaf material may form a greater fraction of the total litter fall in low scrub forest than in the taller forest. However, since the samples were not collected simultaneously in both stands, it is not possible to reach a definite conclusion on this matter. Table 5 does illustrate, however, that litter fall is never very heavy in these forest communities — an average figure would not exceed six grammes per square yard per month. The areas which are not available for

TABLE 5.
*Litter Fall in* Eucalyptus–Angophora *Forest Communities.*

| Formation. | Season of Sampling. | Average Litter Fall. (g./sq. yd./month.) | Litter Composed of Leaves. (%) |
|---|---|---|---|
| Low scrub forest .. | July–November .. .. | 3·65 | 56·3 |
| | November–January .. | 3·00 | 90·2 |
| | January–April .. .. | 2·80 | 62·0 |
| | April–August .. .. | 1·50 | 45·0 |
| | August–September .. .. | 6·20 | 83·0 |
| | September–October .. | 17·30 | 75·5 |
| Tall scrub forest .. | March–May .. .. .. | 1·50 | 31·3 |
| | May–July .. .. .. | 2·65 | 13·6 |
| | July–November .. .. | 5·70 | 40·0 |
| | November–March .. .. | 1·50 | 25·0 |

tree litter accumulation are the majority of rock surfaces (i.e. all other than those which are horizontally placed) and the areas occupied by the tree trunks and the low-growing shrubs. In view of these considerations, only 65–70% of the total area is available for the accumulation of tree litter. The annual accumulation on an acre basis would therefore amount to approximately 500 lb.

It is interesting to compare the litter fall from *Eucalyptus–Angophora* dominants with that collected in an almost pure stand of *Casuarina littoralis* forest which also occurs in localized patches on Hawkesbury Sandstone. Inspection of the morphological character of *Casuarina* cladodes suggests that the canopy is gradually replaced during each year. The quantities of litter collected in a *Casuarina* stand are shown in Table 6, where an average fall of approximately 200 grammes per square yard per month is indicated, at least over a period of seven months.

Table 5 shows that where the litter was collected at monthly intervals from August to September and particularly from September to October in the low scrub forest, the litter fall was heavier than at other seasons. The collection of litter at

TABLE 6.
*Litter Fall in* Casuarina littoralis *Stand.*

| Period of Sampling. (Month.) | Season of Sampling. | Litter Fall. (g./sq. yd.) | Average Litter Fall. (g./sq. yd./month.) |
|---|---|---|---|
| 1 | August–September .. .. | (*a*) 228<br>(*b*) 331 | 280 |
| 4 | September–January .. .. | (*a*) 1560<br>(*b*) 1176 | 342 |
| 2 | January–March .. .. | (*a*) 266<br>(*b*) 473 | 185 |

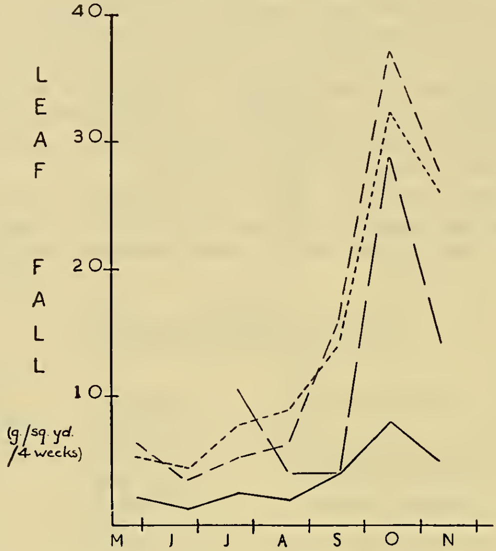
relatively long and irregular intervals — such as the four-month periods from July to November in both low and tall scrub forests — is likely to mask the occurrence of a heavy fall during a relatively short period within that interval. Subsequently, Turner (1954) made a preliminary and more detailed study over a period of six months of litter fall in the Sydney district in rainforest and wet sclerophyll forest occurring on Narrabeen shales and dry sclerophyll forest on Hawkesbury Sandstone. In all three formations, Turner found that leaf fall was heaviest in October. His graphs for leaf fall are reproduced (Text-figure 1) and show the small quantities of litter falling in the sandstone community as contrasted with the others. Turner found "no appreciable and definite trends" with season in twig falls. His values for the leaf, twig and total litter fall in the sandstone community studied are given in Table 7, and show general agreement with those given in Table 5.

In addition to leaf and twig returns, flower, fruit and seed litter must also be considered. For an accurate estimate, samples need to be collected throughout the year; but the majority of species flower in August and the fruit is close to maturity in November. Samples were therefore collected from the living plants in November and consist of the remains of the flowers and the fruits, some of which had matured and opened, while others were still green. The results are shown in Table 8.

It is difficult to express this fraction as an annual addition on an area basis, since many of the shrub species form large woody fruits which may be retained, even after dehiscence, for several years. Firing is frequently responsible for the opening of fruit which has long been mature but dormant. Other species form abundant fruit of a leathery nature. In addition, the seed of different species shows great variation, but a considerable mass of seed may be formed on both small and large seeded varieties. A quantity of about 60 lb. per acre per annum is suggested for the flower, fruit and seed litter from the shrub stratum. The woody fruits of the trees were found in the litter trays and are included in the leaf and twig litter fraction.

Discussion of Data.

Detailed investigations of litter fall collected over a period of several years are required before figures for bulk fall and nutrient returns may be recorded with certainty. Kittredge (1948) gives several examples of variation in annual leaf fall




Text-fig. 1.—Taken from Turner (1954). Leaf fall (g./sq. yd./4 weeks) in rainforest, wet sclerophyll and dry sclerophyll formations in the Sydney district.

- - - -: rainforest; —— ——: rainforest; ———— ————: wet sclerophyll forest; ————————: dry sclerophyll forest on Hawkesbury Sandstone.

M, J, J, A, S, O, N: period May-November during which samples were collected.

in different years in the same stand and includes an instance in Scotch pine forest in Germany, where, in the records of seven years' falls, the maximum fall was three times the minimum.

TABLE 7.
(Taken from Turner, 1954.)
*Litter Fall in Dry Sclerophyll Forest.*

| Date of Sampling. | Leaf Litter. (g./sq. yd.) | | Twig Litter. (g./sq. yd.) | | Total Litter. (g./sq. yd.) |
|---|---|---|---|---|---|
| | Two Weeks. | One Month. | Two Weeks. | One Month. | One Month. |
| May 28 .. | 0·95 | 1·90 | 4·10 | 9·20 | 11·1 |
| June 11 .. | 0·95 | | 5·10 | | |
| June 25 .. | 0·40 | 1·00 | 0·55 | 1·50 | 2·5 |
| July 9 .. | 0·60 | | 0·95 | | |
| July 23 .. | 0·85 | 2·20 | 0·65 | 2·80 | 5·0 |
| August 6 .. | 1·35 | | 2·15 | | |
| August 20 .. | 0·60 | 1·70 | 1·20 | 3·95 | 5·65 |
| September 3 .. | 1·10 | | 2·75 | | |
| September 17 .. | 1·35 | 3·65 | 0·85 | 4·20 | 7·85 |
| October 1 .. | 2·30 | | 3·35 | | |
| October 15 .. | 2·90 | 7·95 | 1·65 | 4·55 | 12·50 |
| October 29 .. | 5·05 | | 2·90 | | |
| November 12 .. | — | 4·65 | — | 4·20 | 8·85 |
| November 26 .. | — | | — | | |
| Total .. | | 23·05 | | 30·40 | 53·45 |

Information is not yet available for Hawkesbury Sandstone communities as to the extent of the effect of wind and rain and other climatic influences on litter fall and on its nutrient content. Until this is obtained, litter fall results over any short period must be considered unique, rather than typical, since they are the product of the interaction of a particular set of environmental conditions on particular individuals. While bearing this limitation in mind, and noting the agreement of Turner's data (Table 7) with that given in Table 5, a figure may be suggested tentatively to represent the annual litter return in these forest communities. No heavy litter falls occurred in the period of the year over which Turner's collections did not extend (December to mid-May inclusive) (Table 5), and therefore a value of approximately 700 lb. per acre would represent the annual litter return from bark, leaf, twig, flower, fruit and seed from trees and shrubs. This figure includes only the usual litter fractions; it must be noted, however, that death of shrubs, caused by insect attack, and death of

TABLE 8.

*Potential Litter from Flower, Fruit and Seed Sources in Shrub Stratum.*

Samples collected from living plants in November, when most of the fruit is mature.

| Formation. | Flower, Fruit and Seed. (g./sq. yd.) |
|---|---|
| Low scrub forest .. .. .. | (*a*) 6·8 |
| | (*b*) 2·9 |
| | (*c*) 4·9 |
| Tall scrub forest .. .. .. | (*a*) 15·2 |
| | (*b*) 14·1 |
| | (*c*) 27·4 |
| | (*d*) 3·4 |
| | (*e*) 11·8 |

large limbs of trees is of quite normal, though spasmodic, occurrence and is not included in the above-mentioned figure. It is of interest to note that the annual litter fall and organic matter production figures, each of which have been calculated from different data and observations, coincide exactly (0·31 ton per acre). This agreement strengthens the possibility that the assumptions approach the actual values; perfect agreement is not anticipated, since so many factors are involved and therefore no special significance is attached to it.

Table 5 shows that the mass occupied by bark, fruit and twigs (100 – leaf litter %) is very appreciable, especially in the tall scrub forest. Turner (1954) estimated that leaf mass in the stand of low scrub forest which he examined occupied only 43% of the total fall. He found that twig fall was relatively much more important in the sclerophyll communities, and especially in dry sclerophyll forest, than rainforest stands — both as regards the dry weight returned and also the nutrient return.

Reference to Tables 2 and 3 shows that of the leaf fall, *Angophora* forms at least approximately 50% and usually much more of the total mass. It therefore was analysed separately from the remainder for nitrogen. These analytical data together with that of twigs, of a mixed leaf sample, and of mature fruit and seed were presented in Tables 15, 17 and 18 (Hannon, 1956).

Of the total annual litter fall of approximately 700 lb. per acre per annum, assuming that 250 lb. represents leaf litter averaging 5,000 p.p.m. nitrogen, and that 450 lb. represent twig, fruit, seed and bark fall from trees and shrubs, averaging 3,000 p.p.m. nitrogen, an annual cycle of only 2·6 lb. nitrogen per acre might be anticipated. It will be shown that the annual return of litter in Hawkesbury Sandstone communities is below the average of figures given in the literature; in consequence this value for the annual nitrogen return is also low.

Estimates of the total vegetative cover in low scrub forest are, according to the topographic position of the stand, 10–40 tons per acre of dry matter; 60–120 tons per acre is the yield in tall scrub forest. In light of these figures, the value for the annual litter production, 0·31 ton per acre, represents only a small fraction of the total plant mass and an exceedingly small fraction of the total nitrogen content of the ecosystem. Leaf-bearing twigs of diameter up to approximately one inch, which include the fractions most commonly found in the fallen litter, have been separated from the crowns of trees felled in areas of sandstone which are being cleared. The observed annual litter fall occupies 5–10% of the mass of this fraction.

Inspection of the morphological character of several shrub species indicates that the usual life span of leaves would be 3–4 years. *Casuarina* appears to replace its foliage annually. Jacobs' (1936) investigations indicate that the life of *Eucalyptus* species leaves is short by comparison with other evergreens. Of the species studied, only *Eucalyptus haemastoma* occurs on Hawkesbury Sandstone and its leaves are considered to have an average life span of not longer than 18 months. Some leaves lived 2–3 years, a few longer, but the average was surprisingly short. These results were obtained from trees growing at Canberra, where environmental conditions are markedly different from those of the sandstone communities. Saplings of *Eucalyptus piperita*, another sandstone species, showed a similar life span. Jacobs records that the life span is affected by position in the crown, bursts of growth, and flowering, insect attack and species. Jacobs has shown that if general conditions are equal, leaves fall from more rapidly growing crowns more quickly than from slow growing ones. He remarks: "The tendency for some species to hold leaves longer than others is probably partly a function of growth rate, and partly a genetical character."

It is considered that the average life span of 18 months for *Eucalyptus haemastoma* leaves as was found in Canberra cannot apply to this species when growing in the Sydney habitat. On an 18 months' life span, approximately 60% of the canopy would be renewed annually. It is difficult to reconcile this estimate with observed leaf fall for species of *Eucalyptus* and *Angophora* in the Sydney district. The above-mentioned value of 10% of canopy probably is closer to the correct value for individuals in these communities.

No information strictly comparable with sandstone forests is available. The only other work that has been done in *Eucalyptus* forests is in Canberra, Western Australia and Victoria. Jacobs (1936) estimated that the alpine ash (*E. gigantea* Hook.) contained 5,800 lb. per acre of oven-dry weight of foliage in the tree canopy and that 15–20 tons of litter (leaf litter and branch shed) is dropped in ten years by the canopy of a fully stocked stand.

In virgin jarrah forests (*E. marginata*) of 105–115 feet height, 50–60% of the total litter fall occurs between January and March and leaves form approximately 50% of the total of approximately 2,100 lb. per acre. Hatch (1955) estimates a return of 9·20 lb. nitrogen per acre per annum, of which 5·23 lb. is contributed by leaf fall.

In a 220-year-old mature *Eucalyptus regnans* forest of trees 250 feet in height, Ashton (private communication) collected an average of 7,208 lb. dry weight of litter per acre per annum over a four-year period; this amount contained 53·5 lb. nitrogen. Leaf fall from *E. regnans* alone contributes 22·2 lb. nitrogen.

The Western Australian and Victorian work is in close agreement as to the main season of leaf fall. Both sites are further south than Sydney, where the maximum litter fall apparently occurs in October. Very great differences in the quantity of total litter fall occur between the different forests, but this is a reflection of the differences in their quality.

In hardwood forests of Southern Carolina Piedmont, Metz (1952) records that litter returns were 4,000–5,000 lb. per acre for the single year during which collections were made. Chandler (1941, 1943) records 2,425–3,020 lb. per acre of litter in the deciduous hardwood forest stands of North America and this includes a return of 16·6 lb. nitrogen per acre. In the evergreen coniferous forests, 2,463 lb. per acre of litter containing 23·6 lb. nitrogen were recorded.

Handley (1954) and Scott (1955) have provided extensive reviews of the literature on this subject. By comparison with all other forests, the litter fall in the sandstone communities is very low.

*Litter Decomposition.*

Jacobs (1936, 1955) remarks that *Eucalyptus* leaf litter disintegrates "fairly quickly by world standards". He points out that the rate of disintegration varies with climate, being faster in warm, moist localities and slower in cold or dry areas. It is of interest to note Kittredge's (1948) comment also: "Most of the species of *Eucalyptus* introduced into the United States form little or no forest floor, and the question may be raised whether these species have the beneficial effect on the soil that is attributed to most other genera."

Presentation of Data.

Despite the low rate of litter fall, the litter layer on the forest floor is always well developed. In the sandstone communities the litter consists mostly of whole leaves. It is only just above ground level that the leaves are broken into smaller pieces. This is suggestive of chewing action by animals rather than enzymatic decomposition by fungi and bacteria. The depth of litter is variable, not only between different formations but also within single stands. It usually is of only one inch depth, but in localized pockets it may accumulate to four inches. The mass of litter from the forest floor is shown in Table 9 and provides evidence suggesting a slow rate of litter decomposition. The samples were collected in typical stands and represent quite average samples of the general litter cover. The samples were dried and sieved to remove sand grains, especially from the lower layers where the leaf material is broken into fragments. The values in Table 9 represent the total litter on the ground (leaves, twigs and bark) and show no definite trend with season. As has already been mentioned, although leaf fall rose in October, the twigs showed no definite seasonal pattern. The total litter fall does not appear to exhibit a cyclic nature as it does in Western Australia, Victoria or in overseas deciduous forests. More critical investigations of the litter mass on forest floors in various seasons would be of interest, but it appears that since only a small fraction of the total is decomposed each year, variation in sampling may mask the incidence of seasonal effects.

TABLE 9.
*The Mass of the Forest Floor.*

| Formation. | Date of Sampling. | Mass of Forest Floor. (g./sq. yd.) |
|---|---|---|
| Low scrub forest .. .. | 28th November .. | 508 |
| | | 778 |
| | 4th March .. | 1580 |
| | | 704 |
| | | 987 |
| | 20th September .. | 884 |
| | | 670 |
| Tall scrub forest .. .. | 4th March .. | 1892 |
| | | 1476 |
| | | 853 |
| | 20th September .. | 1516 |
| | | 1008 |

Discussion of Data.

Owing to the limited areas where litter may accumulate, the values in Table 9 require correction for conversion to an acreage basis. However, taking a figure of 1,000 grammes per square yard as an average value of the quantity of accumulated litter and assuming a rate of 70 grammes per square yard per annum (based on figures given in the preceding section), accumulation of litter has obviously proceeded over a period of 14 years. Periodic occurrences of adverse environmental conditions, such as severe drought, may be responsible for exceptionally heavy litter falls and contribute largely to the quantities of litter found on the forest floor. During occasional gales, twigs with living leaves still attached, are frequently torn from tree tops. Very heavy falls of scorched leaves have been observed immediately after bush fires. Such occurrences would reduce the estimate of 14 years as the period during which litter accumulates. Even allowing for these occurrences, however, and even were some nutrients liberated when the litter eventually reached the ground surface and decomposition began, certain amounts of nutrients must be locked within the litter for long periods. Specht (1953) finds that in sclerophyllous heath vegetation in South Australia, nitrogen and phosphorus are not liberated until decomposition is complete.

By studying the mass of the forest floor in several stands of *E. marginata* which had been protected from fire for varying periods, Hatch (1955) records that after twenty years' protection, which was the maximum period studied, the forest floor was still accumulating and the equilibrium between litter fall and litter decomposition

TABLE 10.
(Taken from Jenny *et al.*, 1948.)*
*Weights of Forest Floors in the United States.*
(Mostly on oven-dry basis.)

| Locality. | Vegetation. | Number of Samples. | Weights of Forest Floor. (lb./acre.) | |
|---|---|---|---|---|
| | | | Range. | Average. |
| Minnesota and Wisconsin | Basswood, maple, aspen, birch. | 16 | 25,050–59,787 | 39,556 |
| Connecticut .. .. | Hardwoods. | 5 | 7,000–94,000 | 60,244 |
| Fern Canyon (California) | Chapparral. | 101 | 10,000–47,000 | 33,200 |
| Ohio, Indiana .. .. | Sassafras, black locust. | ? | 6,800–10,200 | 8,500 |
| Ashville (North Carolina) | Pine, oak. | 2 | 6,300 7,900 | 7,100 |
| South Appalachians .. | Hardwood. | 5 | 3,146–16,359 | 10,435 |
| Victoria, Australia .. | *Eucalyptus regnans.* | — | — | 20,070 |
| Western Australia .. | *E. marginata.* | — | — | 20,160 |
| Sydney, N.S.W. .. .. | *Eucalyptus–Angophora.* | — | — | 5,600 |

* Values for three types of Australian *Eucalyptus* forest are included for comparison.

was not yet attained. At this time of 20 years' protection, 4½–6½ tons of litter had accumulated per acre. He suggests 4½ tons from a canopy cover of 35% (a stand of 55–65 feet in height) and 6½ tons from 50% cover. Where the canopy was complete, 9 tons had accumulated after 20 years' protection.

Ashton (private communication) collected 20,070 lb. per acre in the total litter fraction of the mature *E. regnans* forest floor. The ratio of the total floor to the annual litter fall was only 2·54, indicating a rapid decomposition of the litter.

It is of interest to compare the mass of the sandstone forest floors (average of 5,600 lb. per acre) and the figures of Hatch and Ashton given above with the data summarized by Jenny, Bingham and Padilla-Saravia (1948) and given in Table 10. Scott (1955) has provided an extensive review of the literature on this subject also.

Kittredge (1948) notes that the total forest floor accumulation as compared with the annual litter fall may vary between a ratio of 1 or less in the tropics, where litter is decomposed very rapidly, and 60, as is found in the birch–sugar maple–spruce forest in northern New Hampshire. In this area, the mass of the total forest floor has a value of 120 metric tons per acre. The ratio varies commonly between 3 and 15, and is essentially a measure of the rate of the decomposition of litter. Where equilibrium between accumulation and decomposition has been attained, the ratio also represents the number of years for the establishment of that equilibrium. Jenny, Gessel and Bingham (1949) have applied certain refinements to these latter principles in their comparative study of the decomposition rates of organic matter in temperate and tropical regions.

The agencies which are active in litter decomposition in the sandstone communities other than *Casuarina* stands have received no attention. It is to be expected that the low moisture and nutrient levels would limit the activity of microorganisms, including the animal population, just as it does the development of the plant cover. Clark (1950) has paid attention to the role of the animal populations in *Casuarina* decomposition, and several workers—Fenton, Fraser (1948), Anderson (1948), Coogan (1949). Simons (1950), Carne (1950)—under the leadership of Burges, have examined the fungi and bacteria which are engaged in *Casuarina* decomposition. Clark (1950) found that the fauna is very similar to that of pine forests in Europe, both in respect of species and numbers of animals present. It has already been pointed out that *Casuarina* grows in almost pure stands where the heavy litter layer allows greater retention of moisture than in *Eucalyptus* forests. The faunal population of the latter may resemble that of the humus layers of regenerating jarrah forest which have been investigated by McNamara (1955). He reports a similarity in numbers and composition of the insect fauna in these forests with those in Danish beechwoods and North American hardwood forests, but the absence of the high proportion of earthworms.

## General Discussion.

The evidence presented indicates that organic matter production and litter and nitrogen returns in the *Eucalyptus* forests on Hawkesbury Sandstone are small by comparison with other forests. In addition, the forest floor is not so well developed as in many other types of forests; although decomposition is relatively slow in the sandstone forests, *Eucalyptus* forest is generally considered to show a rapid rate of litter decomposition by world standards. The evergreen, broad-leaved and sclerophyllous *Eucalyptus* forests are thus of a different nature from those found in other areas.

It would be of interest to compare the ratios of the nutrient content of soil:plant: litter in *Eucalyptus* forests with the hardwood, coniferous and deciduous types of forests. Such a comparison would clarify whether the differences in the nutrient circulation mentioned above are a reflection of a smaller nutrient capital in the ecosystem or a different proportion between the three fractions. It is possible that a greater percentage of the capital is "mobile" in other forest types, thus allowing the exercise of a less rigid economy.

The quantities of nutrients contained in ecosystems have received no attention until recently. Estimates of the absolute nutrient content had been made on only separate aspects of the ecosystem such as the litter or the soil. There is much to recommend the simultaneous examination of all three fractions of the ecosystem, since such an approach involves the synthesis of otherwise isolated observations and emphasizes the functioning of the ecosystem as the entity it is. The employment of expression in absolute rather than relative terms also offers several advantages. Not only are such values mentally digestible, but they avoid the deception which concentration values frequently present.

In connection with the afforestation programme of the *Calluna* moors, Rennie (1955) has made an outstanding and valuable contribution involving this approach. He examined the original records of analytical data on the composition of the organs of individual mature temperate forest trees and in the thinnings. By combining these data with records of the density of wood, growth rate of trees and yield per acre of forest stands, he estimates and fractionates the calcium, potassium and phosphorus content of pine, other conifer and hardwood forests into the component plant organs in the main timber stand and the thinnings. He notes that only seldom have nitrogen analyses been recorded, but includes those that are available. By this means he assesses the nutrient demands of pine and birch stands and compares these with that of *Calluna*. An evaluation of the ability of *Calluna* soils to provide for the nutrient demands of the pine or birch is thus possible.

Table 11 is based on Rennie's compilation of data relating to nitrogen. The available information allowed the calculation of the nutrient content of the plant cover and soil, but the litter fraction had to be ignored in some instances. The estimated nitrogen content of the fractions of the Hawkesbury Sandstone ecosystem is included

TABLE 11.
(Partly after Rennie, 1955.)
*The Fractionation of Nitrogen in a Variety of Ecosystems.*

| Nature of Stand. | Yield. (ton/acre.)* | Total Nitrogen Content. (lb./acre.)* | | | Plant N Content.‡ / 0–50 cm. Soil N Content Ratio. | Nitrogen Content of Soil+Plant. (lb./acre.) |
|---|---|---|---|---|---|---|
| | | Soil.‡ | | Plant. | | |
| | | 0–25 cm. | 0–50 cm. | | | |
| Agricultural annual crop .. .. .. .. | — | 4,500 | 6,355 | 64 | 0·010 | 6,419 |
| Scots Pine Forest, 150 years old .. .. | — | 2,850 | 5,000 | 551 | 0·110† | 5,551 |
| *Calluna* moor .. .. .. .. .. | Plant .. 4·9<br>Litter .. 1·7 | 2,984 | 3,442 | Plant .. 88<br>Litter .. 37 | (Plant+litter N)/(0–50 cm. soil N) .. 0·036 | +Litter .. 3,567 |
| Pine afforested moor, 80 years old.. .. .. | —<br>Litter .. 14·7 | 3,471 | 3,742 | Plant .. 441<br>Litter .. 419 | (Plant+litter N)/(0–50 cm. soil N) .. 0·290 | +Litter .. 4,602 |
| *Eucalyptus* forest on Hawkesbury Sandstone .. | Plant .. 70·0<br>Litter .. 2·5 | 0–21 cm.<br>917 | 2,021 | Plant .. 353<br>Litter .. 11 | 0·175<br>(Plant+litter N)/(0–50 cm. soil N) .. 0·180 | +Litter .. 2,385 |

* Values are converted from Rennie's expressions of kg./acre.
† This figure is entered as 0·18 in Rennie's table, but consultation of his original data reveals that 0·11 is the correct value.
‡ In the Hawkesbury Sandstone communities, "soil" is replaced by "rock+soil".

for comparison. Inspection of this table shows that the nitrogen content of the Hawkesbury Sandstone ecosystem is lower than any of the others listed.

Another feature of considerable interest in the *Eucalyptus* forest is the plant nitrogen content : rock and soil nitrogen content ratio value. It is in excess of all values other than the pine-afforested moor community, which would appear to be incapable of survival, if dependent on only the naturally occurring nutrient supply of the *Calluna* moor soil. Comparison with the Scots Pine Forest stand would be of greater significance, since the latter is a naturally occurring and somewhat similar formation. It appears that the *Eucalyptus* forest plant cover is making a greater demand on the soil reserve of nitrogen than does the pine forest. However, Rennie does not include a value for the nitrogen content of the litter fraction in the Scots Pine Forest. Since these forests have such a well-developed litter layer, which contains considerable quantities of nutrients, it is illogical to exclude it from the calculation. Presumably, its value would approximate that given for the pine afforested moor; in this instance, the ratio of plant + litter N : soil N would become very similar in the pine and *Eucalyptus* forests. The chief difference thus lies in the proportion of nutrient immobilized in the litter layer. The litter fraction of the sandstone ecosystem occupies only a minor fraction in comparison with the *Calluna* moor stands and especially the pine forests. When nutrient balance is under consideration, the logic of Rennie's grouping of the fractions of the ecosystem into plant + litter as opposed to soil is open to question. The litter fraction forms part of the reserve upon which the plants draw for their nutrient requirements. Considerable proportions of the root systems are located in the litter layer of pine forests. On this basis the ratios of plant nitrogen content : soil + litter nitrogen content values are:

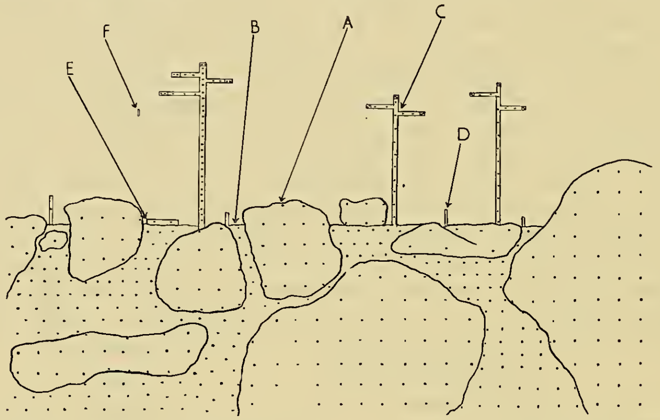
| | |
|---|---|
| *Eucalyptus* forest .. .. .. | 0·174 |
| Pine forest .. .. .. .. .. .. | 0·102 |

The abovementioned suggestion that the eucalypt forest plant cover makes a greater demand on the nitrogen reserves of the ecosystem than does the pine forest would therefore appear to be a valid conclusion, especially since more than 50% of the rooting medium nitrogen content is bound within undecomposed parent material; elimination of the nitrogen content of the rock increases the ratio of plant : "true soil" to 0·354. This character possibly is the key to the differences in nutrient circulation previously noted between *Eucalyptus* and other forests.

This character of the *Eucalyptus* forest as contrasted with other ecosystems may also be reflected in other nutrient elements such as phosphorus, potassium and calcium. Evidence to be presented later suggests that the demand made by the plant cover on the soil for calcium is even greater than that for nitrogen. This is a matter urgently in need of investigation at the present time, when Australian ecologists are emphasizing the possibility that the sclerophyllous character of the native vegetation may be determined by low levels of nutrient supply.

Rennie (1955) has shown that the quantities of all three nutrients, calcium, potassium and phosphorus, taken up by forest growth decrease in the order: hardwood, coniferous other than pine, and pine forest. "All three types of forest take up considerably less potassium and phosphorus compared with agricultural crops, but the amounts of calcium are not greatly less; moreover, as all except very young forest growth differs from agriculture in taking up calcium and not potassium, in greater amount, the importance of calcium to forest growth appears to have been markedly under-estimated." It is of interest to note that in her studies of litter decomposition in *Casuarina* stands on Hawkesbury Sandstone, Fraser (1948) has suggested the occurrence of a vigorous calcium cycle in these communities. In investigations of the composition of eucalypt forest litter, Turner (1954) has also noted that the calcium and potassium content of the leaf litter in dry sclerophyll *Eucalyptus* forest communities, when expressed on a concentration basis, exceeds that in the wet sclerophyll forest stand studied which occurred on the fertile chocolate loam of the Narrabeen series. In these areas the nutrient and water supply are at very favourable levels for plant growth. Since litter fall in wet sclerophyll forest communities exceeds by a factor of 2·6 that of the dry sclerophyll, the absolute amounts of all nutrients in the total litter fall are less in dry than wet sclerophyll forest. Both concentration and absolute values for phosphorus in the litter were much lower in dry than wet sclerophyll communities.

Features of the circulation of nitrogen in the Hawkesbury Sandstone ecosystem which have been discussed above are summarized in Text-figure 2. Both the mass of each fraction and its nitrogen concentration have been plotted quantitatively, the mass of each fraction being proportional to the area it covers, and the nitrogen concentration being proportional to the density of the stippling. The diagram thus gives a graphic representation of the very small proportion of nitrogen present in concentrated form in the ecosystem, since the great bulk is locked within the soil




Text-fig. 2.—The fractionation of nitrogen in a Hawkesbury Sandstone ecosystem. A: Undecomposed parent material; B: Soil; C: Tree stratum; D: Shrub stratum; E: Litter accumulated on forest floor; F: Annual litter fall.

The mass of each fraction is proportional to the area it covers, and its nitrogen concentration to the density of the stippling; consequently it has not been possible to represent accurately the relative volume of each fraction, e.g., tree height is grossly underestimated in comparison to soil depth. Refer to pp. 66-67 for details of the calculation.

and woody tissue; it also shows the very small proportion that is "mobile"—that is the proportion involved in the annual circulation of nitrogen within the community.

While thus a closed cycle of nutrient movement will exist in the Hawkesbury Sandstone communities as in all virgin communities, and while on theoretical grounds a mature community exhibits no net gain or net loss, a realization of 100% efficiency is most improbable, particularly when so many transfers of the nutrients from one form to another and from one phase of the ecosystem to another are involved. A state of equilibrium exists in which processes tending towards the impoverishment of the nutrient status, if not completely counterbalanced by nutrient release from the weathering of the parent rock or by external accessions, at least proceed extremely slowly. The sources of loss and gain of nitrogen in these communities require examination and these studies will be reported later.

## *APPENDIX.*

### The Density of Hawkesbury Sandstone and the Apparent Density of Sandstone Soils.

#### *Methods.*

Weighed rock fragments were coated with a thin layer of paraffin wax and immersed in a known volume of water in a measuring cylinder. A glass rod was used to remove all air bubbles from the rock surface and the volume of displaced water measured. Measurements of the rock pieces are shown in Table i.

No special sampling tool designed to provide for apparent density measurements of soil samples by standard methods was available. Tins used for the storage of particular types of foodstuffs and consequently of uniform dimensions were therefore opened at one end and punched with a small hole to allow for an air vent at the other.

A pit was dug and the tins were placed horizontally at various depths down the exposed profile. A wooden block was used to cover the tins and hammered carefully so that the tins were driven into the soil profile just to their full depth. By this method, little, if any, compaction of soil occurred. Soil blocks containing the tins filled with soil were then dug out. The soil was cut level with the top of the tin, carefully removed, dried out and weighed. Density values were calculated by comparing the values of the dried mass of soil with the volume contained by the tin. Values of samples from various depths in several formations are shown in Table ii.

TABLE i.

*Mass, Volume and Density Values of Fragments of Hawkesbury Sandstone.*

| Sample Number. | Mass. (g.) | Volume. (c.c.) | Density. (g./c.c.) |
|---|---|---|---|
| 1 | 18·8 | 8·5 | 2·21 |
| 2 | 36·1 | 17·5 | 2·06 |
| 3 | 36·5 | 18·0 | 2·03 |
| 4 | 69·1 | 31·0 | 2·23 |
| 5 | 105·3 | 50·0 | 2·11 |
| 6 | 167·0 | 79·0 | 2·11 |

ANALYSIS OF WOODY TISSUE OF HAWKESBURY SANDSTONE SPECIES.

Details of the nitrogen and carbon content of the bark-free wood of several species are shown in Table iii. As in the leaf and seed tissue values previously recorded, the wood of the legume species has a much higher nitrogen content than the non-legumes. Although the living tissue in wood forms only a small proportion by mass, it contains proteins and sugars, whereas the lignified cells are empty. It would thus be a proportionately greater contributor to the nitrogen content of the wood sample. Russell (1950) notes that the lignins of leguminous plants are usually richer in their nitrogen content than non-legumes. Apparently this, together with higher nitrogen levels in the living cells of legumes, is responsible for the legume carbon-nitrogen ratio, which is markedly lower than that of the others. The two species of highest carbon-nitrogen ratio, *Banksia serrata* and *Eucalyptus paniculata*, have

TABLE ii.

*Mass and Apparent Density of Hawkesbury Sandstone Soil.*

Samples were collected at various depths in profiles located in several formations.
Tins of a volume of 230 c.c. were used throughout the sampling.

| Formation. | Depth of Sample. (in.) | Mass. (g.) | Apparent Density. (g./c.c.) |
|---|---|---|---|
| Shrub swamp .. .. .. | 1 – 3¾ | 289 | 1·26 |
| | 4¼– 7 | 271 | 1·18 |
| Sedge swamp .. .. .. | 0 – 3 | 294 | 1·28 |
| | 3 – 6 | 317 | 1·38 |
| | 10 –13 | 332 | 1·44 |
| | 18 –21 | 348 | 1·51 |
| | 30 –33 | 396 | 1·72 |
| Low scrub forest .. .. | 0 – 2¾ | 326 | 1·42 |
| | 9¼–12 | 351 | 1·53 |
| | 15¼–18 | 333 | 1·45 |
| Tall scrub forest .. .. .. | 0 – 3 | 309 | 1·34 |
| | 16 –19 | 348 | 1·51 |
| | 25 –28 | 334 | 1·45 |
| | 33 –36 | 366 | 1·59 |

density values of approximately twice that of the other species. It is likely, therefore, that differences in the carbon and nitrogen values could be correlated with anatomical detail, if it were available.

Records of the nitrogen content of wood are not numerous, but it appears that the values shown in Table iii are typical. Ramann (1890), quoted by Lutz and Chandler (1949), reported the nitrogen content of wood as 1,000–5,000 p.p.m.; Kalnins and Liepins (1938) found that Scotch pine wood contained 1,200–1,600 p.p.m. Converting the protein values of sapwood given by Wise and John (1952) to nitrogen by the conventional factor of 6·25, the content of the following species is:

Ash (*Fraxinus elatior* L.) .. .. 2,192 p.p.m. N.
Elm (*Ulmus sativa* Mill.) .. .. .. 2,768 p.p.m. N.
Scotch pine (*Pinus sylvestris* L.) .. 1,328 p.p.m. N.

TABLE iii.
*The Concentration of Nitrogen and Carbon in Bark-Free Wood.*

| —— | Total Nitrogen. (p.p.m.) | Organic Carbon. (p.p.m.) | Carbon : Nitrogen Ratio. |
|---|---|---|---|
| PROTEACEAE | | | |
| *Banksia serrata* .. .. | 1,024 | 472,446 | 461 |
| MYRTACEAE | | | |
| *Angophora costata* .. | 2,976 | 460,570 | 155 |
| *Eucalyptus paniculata* Sm. | 1,107 | 507,502 | 459 |
| *E. piperita* .. .. .. | 1,736 | 468,522 | 270 |
| LEGUMINOSAE | | | |
| *Acacia baileyana* F. Muell. | 4,784 | 421,385 | 88 |
| *A longifolia* (Andr.) Willd. | 5,027 | 389,908 | 78 |
| *A. maidenii* F. Muell. .. | 7,913 | 440,000 | 56 |
| CASUARINACEAE | | | |
| *Casuarina torulosa* .. .. | 1,966 | 464,546 | 236 |

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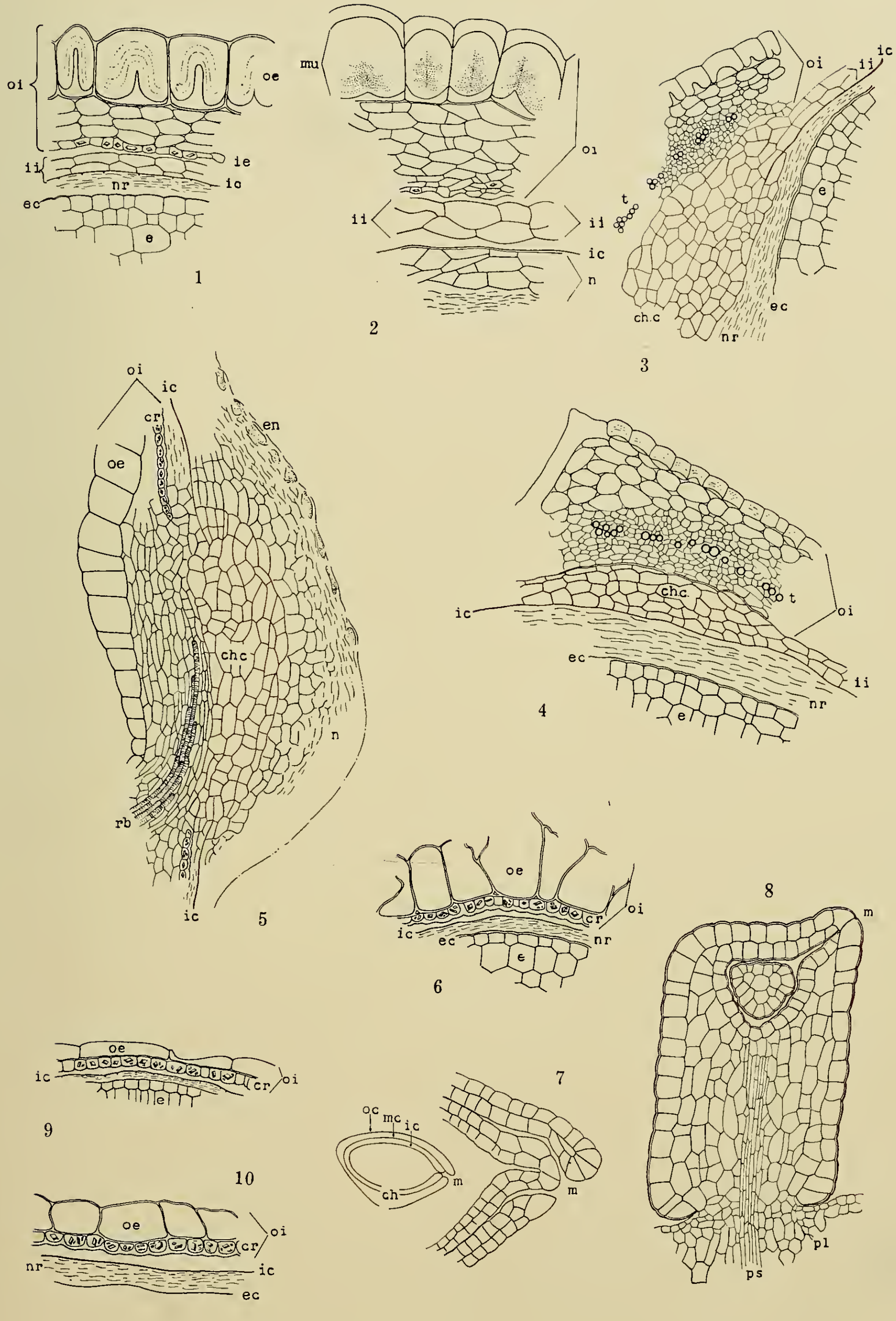


Seed coat anatomy in *Eucalyptus*.